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ELK DISTRIBUTION AND MODELING IN RELATION TO ROADS

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Abstract: We tested performance of 3 aspects of an elk (*Cervus elaphus*)–road density model that has been used extensively throughout western North America but has not been sufficiently validated. First, we tested the hypothesis that elk selection of habitats increases with increasing distance away from open roads. This forms the empirical basis for the model. Second, we compared the model's predictions of relative elk habitat selection, or habitat effectiveness (HE), with observed values at varying levels of road density. And third, we examined the potentially confounding effects of different spatial patterns of roads on model predictions. We conducted our study during spring and summer, 1993–95, at the Starkey Experimental Forest and Range (Starkey), northeast Oregon. Selection ratios were calculated using >100,000 recorded locations of 89 radio-collared female elk, with locations mapped in relation to 0.1-km-wide distance bands away from open roads. Selection ratios increased with increasing distance from open roads, and varied between seasons, but not among years or individual animals. Linear regression models, using distance to open roads as a predictor, accounted for significant variation in selection ratios during spring and summer. Model predictions of HE, as measured by number of elk locations, corresponded only weakly, however, with observed values of HE. The contradictory results of these 2 analyses may be explained in part by our simulation results, which showed that potential reductions in elk HE vary strongly with the spatial pattern of roads, which is not measured by the elk–road density model. Our results suggest that (1) management of roads and related human activities during spring and summer should remain an important consideration for modeling and managing the elk resource; and (2) a spatially explicit road component is needed for elk habitat models.

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Shifts in elk distribution away from roads used by motorized vehicles have been documented across many areas of the western United States (Hieb 1976, Perry and Overly 1977, Lyon 1979, Rost and Bailey 1979, Witmer and deCalesta 1985). Such shifts may reduce carrying capacity of some areas (Wisdom and Thomas 1996) and redistribute elk from public to private lands (Wertz et al. 1996). Roads and associated disturbances have been presumed to be the primary agent driving elk distribution across seasons and landscapes (Leege 1984, Lyon 1984, Lyon et al. 1985). To better quantify this relation, an elk–road density model was developed (Thomas et al. 1979, Lyon 1983) that has been used extensively throughout the intermountain west as a component of elk habitat effectiveness models (Leege 1984; Thomas et al. 1979, 1988; Wisdom et al. 1986).

Habitat effectiveness for elk has been defined as the "percentage of available habitat that is usable by elk outside the hunting season" (Lyon and Christensen 1992:4). The road component of HE models was developed by manipulating data based on indices of elk use (pellet group

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densities) in relation to distance from open roads, but not in relation to open road densities (Lyon 1979, 1983). Although the road density variable and other components of elk HE models have undergone only limited validation (Lyon 1984), these models and their variants have been used extensively in National Forest System planning and management (Edge et al. 1990, Christensen et al. 1993). In addition, the prediction of HE for the elk–road density model assumes no change in HE with variation in the underlying spatial pattern of roads, despite substantial differences in existing road patterns on landscapes where the model is used.

Widespread use of the elk–road density model is likely to continue: elk remain a focal species in land and resource management of National Forests in the interior northwest (Edge et al. 1990, Groves and Unsworth 1993) and are of considerable economic importance (Duffield and Holliman 1988, Loomis et al. 1988, Bolon 1994). Land management plans for National Forests often include specific standards for elk HE values related to road densities or other road management criteria (Carter 1992). Moreover, roads are of increasing concern for wildlife occurring on public lands in the interior northwest (Wisdom et al. 2000), as well as for terrestrial and aquatic communities worldwide (Trombulak and Frissell 2000). Better quantification of effects of roads on elk and other wildlife is needed, because road-related mitigation for wildlife is costly and logistically challenging. Closing or obliterating roads to reduce vehicle access can cost millions of dollars and be politically unpopular; likewise, maintaining open roads may be expensive and controversial.

In response to a long-standing need for validation, we tested performance of 3 aspects of the elk–road density model of Lyon (1983). Our specific objectives were to (1) test the hypothesis that the degree of selection of habitats by elk increases with increasing distance from open roads (test of elk–distance from roads hypothesis), (2) compare model predictions of HE with observed values (evaluation of HE model predictions), and (3) examine potentially confounding effects of different spatial patterns of roads on model performance (simulation of spatial-pattern effect).

STUDY AREA

The Starkey Experimental Forest and Range is a research area of about 101 km^2 in northeast Oregon (Fig. 1A). The Starkey Project was initiated there in 1987; its primary purpose is to support long-term studies of elk, mule deer (*Odocoileus hemionus*), and cattle on summer range in relation to timber and grazing management, recreation, impacts of roads, and road-associated human activities (Rowland et al. 1997). The Starkey area is particularly useful for such ungulate research because it reflects "the history of resource exploitation typical of the ponderosa pine-bunchgrass forests" (Skovlin 1991:1). Also, traffic levels, recreational activities (including hunting), cattle grazing, and timber management resemble patterns of use on adjacent public lands (Skovlin 1991, Rowland et al. 1997).

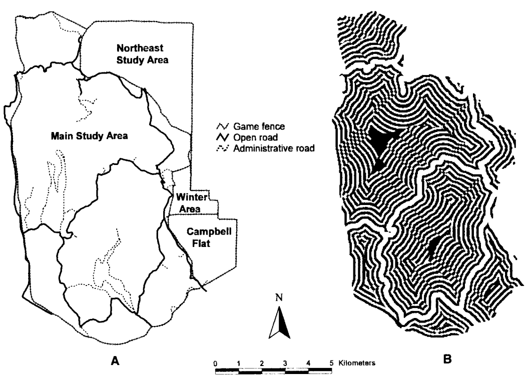

Fig. 1. Study area and roads in the Starkey Experimental Forest and Range, Oregon (A), and delineation of 0.1-km distance bands buffered from open roads (B) for evaluation of elk distribution in relation to roads, 1993–95. In "B" all pixels >1.9 km from an open road were combined in band 2.0; broad, light gray band indicates open road and 0.1 km on either side of road.

To support ungulate research objectives, most of Starkey is enclosed by ungulate-proof fence of New Zealand woven-wire (Bryant et al. 1993, Rowland et al. 1997). Starkey has been divided into 4 areas, each fenced separately (Fig. 1A). Two areas called main (77.6 km^2) and northeast (14.5 km^2) are used for telemetry studies during spring–fall and contain known population densities of mule deer and elk that are managed to meet study objectives (Rowland et al. 1997). Starkey also contains a 265-ha winter area (Fig. 1A), where ungulates are fed at a maintenance level from December to April (Wisdom et al. 1993, Rowland et al. 1997).

Our study was confined to the main area, where about 430 adult elk were present from early April until mid-December each year during our study (1993–95), along with 540 domestic cow–calf pairs and 270 adult mule deer. Densities of adult elk in the study area (5.5/km^2) were similar to those in occupied elk habitat on adjacent public lands (B. K. Johnson, unpublished data). Moreover, habitat available to elk in the main study area was 2–4 times larger than typical summer home ranges of elk in the Blue Mountains (20–29 km^2; Leckenby 1984), thus providing study animals with large-scale habitat choices commensurate with those of free-ranging herds.

During our study, about 44 of 201 km of roads (22%) were open to the public (Fig. 1A). Open roads crossed a variety of slopes, but most were built on gentle terrain (mean slope = 12%). All open roads were single lane (3.5–4.5 m wide) and primarily graveled. Starkey roads are similar to those on adjacent National Forest lands (R. K. Nielsen, U.S. Forest Service, personal communication), and are comparable to the secondary roads defined by Perry and Overly (1977) in their analysis of elk–road relations in the Blue Mountains of Washington and to roads used by Lyon (1983) in his development and refinement of the elk–roads model. The majority of Starkey roads (78%) were closed to the public; however, about one-half of the closed roads were open for administrative use. Administrative roads were typically narrower and only occasionally graveled.

Over 70 traffic counters monitor traffic rates at Starkey (Rowland et al. 1997). Daytime traffic rates on open roads were usually 1–4 vehicles/12 hr, but sometimes exceeded 50 vehicles/12 hr on certain road segments (M. J. Wisdom, unpublished data). Summer traffic rates were consistently higher than those in spring. Traffic rates on administrative roads were much lower than those on open roads, generally $\leq$1 vehicle/12 hr.

Total road density in the main study area was 2.6 km/km^2, with about 0.6 km/km^2 of open roads; road densities were constant during the 3 years of this study. Open road density on National Forests surrounding Starkey was about 1.3 km/km^2, and is steadily declining with intentional closure of roads to meet travel management plan objectives (U.S. Forest Service 1990).

METHODS

Characterizing Road Location and Type

Road locations were verified with a differentially corrected global positioning system (DGPS), mapped as a vector layer, and rasterized in a spatial database of 30- $\times$ 30-m pixels (Rowland et al. 1998). Road data, both spatial and attribute, were entered in a geographic information system (GIS) and digitized into Universal Transverse Mercator Grid System (UTM) coordinates. Three types of roads were designated in the database: open (open to the public); closed (no known vehicle use or physically barricaded); and administrative (restricted vehicle use, not open to the public).

Monitoring Animal Movements

Elk were trapped each year in the winter area (Fig. 1A), as well as in 2 corral traps placed in the main area (Rowland et al. 1997). All animal handling and feeding followed protocols approved by an Institutional Animal Care and Use Committee (Wisdom et al. 1993). Radiocollars were placed on female elk in spring before animals were released into different study areas. Whenever possible, collars were placed on elk that were tracked the previous year. Collars functioned for about 2.5 years, but were replaced whenever an elk was recaptured. The percentage of female elk monitored, relative to the total adult female population in the study area, ranged from 12–19% during our study.

Locations were generated with the use of a LORAN-C automated telemetry system (Dana et al. 1989, Findholt et al. 1996, Rowland et al. 1997, Johnson et al. 1998). The telemetry system was activated each year from early April until mid-December. Each telemetry location was assigned to UTM coordinates of the associated 30- $\times$ 30-m pixel. Locations were weighted by a spatially explicit algorithm that corrected for spatial differences in the rate at which telemetry locations were successfully obtained (Johnson et al. 1998). Mean ($\pm$SE) position error for locations was 53 $\pm$ 5.9 m (Findholt et al. 1996).

Elk locations for our analyses were collected during spring (mid-Apr to mid-Jun) and summer (mid-Jun to mid-Aug) 1993–95, resulting in 6 sampling periods (2 seasons $\times$ 3 yr). We did not analyze locations obtained in the fall when hunts were conducted to eliminate potentially confounding effects of increased traffic rates and hunter behavior on elk. Moreover, the elk–road density model was developed primarily from data collected outside the hunting season (Lyon 1983).

More than 100,000 locations were recorded for 32–53 elk that were monitored during these 6 sampling periods, with 1 location/elk systematically collected about every 3–5 hr. Mean (±SE) time interval between locations (3.7 ± 0.6 hr) was similar among elk, and locations from each elk were typically spread evenly across each sampling period. Each elk in our analyses had ≥100 locations per sampling period; however, mean (±SE) number of locations per animal in a period was substantially larger, ranging from 247 ± 15 (n = 36) to 912 ± 40 (n = 33). Turnover rate among radiocollared animals in our samples was >50% (i.e., less than half the elk in our spring samples were also included the previous summer). Only 4 elk from the spring 1993 sample remained in the summer 1995 sample.

Testing the Elk–distance from Roads Hypothesis

All 86,000 of the 30- × 30-m pixels in the main study area were buffered against open roads with the spatial analysis software UTOOLS (Ager and McGaughey 1997) to calculate the distance from recorded elk locations to the nearest open road. Distances were straight-line and represented minimum values. Roads in an 800-m-wide band surrounding the study area were included in the buffer routine to account for open roads outside the fence that might have influenced distributions of elk within the fence (Fig. 1A). Pixels were subsequently grouped into 20 distance bands, each 0.1 km wide (Table 1; Fig.1B). The maximum distance from any pixel to an open road was 2.4 km. For distance-to-roads analysis, locations for each elk were assigned to the appropriate distance band and summed by band for each sampling period.

Each radiocollared elk was treated as a sample unit. This eliminated problems of non-independence that may arise if individual locations are considered samples (e.g., serial correlation of locations collected sequentially from an animal), or if locations are pooled across animals that have different patterns of habitat use (Aebischer et al. 1993, Otis and White 1999). We calculated a selection ratio, USEAVAIL, based on distance bands as our response variable: USEAVAIL = PROPUSE/PROPAVAIL, where PROPUSE is the proportion of use, or number of radiolocations of an elk in a distance band (OBSERVATIONS) divided by the total number of locations for that elk in the sampling period (TOTAL), and PROPAVAIL is the proportional availability of a distance band, i.e., band area divided by total study area. PROPAVAIL was constant across sampling periods and elk. Our ratio is similar to forage selection ratios commonly used in resource selection studies (Manly et al. 1993).

Table 1. Area (ha) in distance bands created for evaluation of elk distribution in relation to distance from open roads, Starkey Experimental Forest and Range, Oregon, 1993–95.

Distance band[a]	Area	Study area (%)
0.1	961	12.4
0.2	774	10.0
0.3	806	10.4
0.4	618	8.0
0.5	634	8.2
0.6	585	7.6
0.7	480	6.2
0.8	388	5.0
0.9	392	5.1
1.0	331	4.3
1.1	265	3.4
1.2	279	3.6
1.3	245	3.2
1.4	212	2.7
1.5	179	2.3
1.6	148	1.9
1.7	123	1.6
1.8	90	1.2
1.9	86	1.1
2.0	172	1.9

[a] Distance bands are in 0.1-km increments. Band 0.1 includes all pixels from 0–100 m from an open road; band 2.0 includes all pixels > 1.9 km from an open road.

Because our dependent variable was a ratio of 2 proportions and violated assumptions of normality and equal variance, we performed an arcsine transformation of the numerator (PROPUSE) to allow for standard statistical analysis (Zar 1984:240):

$$\text{USEAVAIL} = \{\sin^{-1}[(\text{OBSERVATIONS} + 0.375) \div (\text{TOTAL} + 0.75)]^{1/2}\}/\text{PROPAVAIL}$$

The denominator, PROPAVAIL, did not require transformation because it remained constant for each band among seasons and years. Our transformation succeeded in normalizing selection ratios across distance bands, as well as in stabilizing variances.

The transformed selection ratio also was weighted to (1) account for unequal number of locations among elk (i.e., estimates for more frequently located elk were more precise), and (2) restabilize the variance after dividing the transformed PROPUSE by PROPAVAIL (D. B. Marx, University of Nebraska, personal communication):

$$\text{WEIGHT} = \text{PROPAVAIL}(\text{TOTAL})^{1/2}$$

We first tested whether selection ratios (response variable) varied among distance bands or animals (nested within yr) for each sampling period using analysis of variance (ANOVA; PROC GLM, unbalanced design; SAS Institute 1989). Next we pooled all data to test for effects of distance band, animal, year, and season (main effects) on selection ratios with a factorial ANOVA for unbalanced designs. Additional ANOVAs were used to test for year effect within linear models for each season. To overcome the problem of variable sample size for our unbalanced design, we used least square means to test for differences in USEAVAIL among years when a year effect was significant (PROC GLM; SAS Institute 1989).

To develop predictive models for elk selection in relation to distance from roads, we explored the mathematical relation between selection ratio (USEAVAIL), animal, and distance band for each sampling period, including use of polynomial terms up to the 5th degree for distance band (PROC GLM; SAS Institute 1989). We found that the more complex models were statistically significant in all periods ($P < 0.001$ for cubic or higher order terms for distance band), but the simple linear term for distance band also was significant and accounted for 90–97% of the model sum of squares. Consequently, we estimated model parameters for only simple linear models for both seasons (i.e., USEAVAIL on distance band as a continuous variable).

Variance of USEAVAIL was markedly higher in the outer distance bands, despite the transformations, and mean USEAVAIL declined in the outermost 1 or 2 bands in every period. Bands 1.9 and 2.0 were isolated (Fig. 1B), and thus likely to be largely unavailable to many elk in our study area. Consequently, we omitted these 2 bands (which together composed only 3% of the study area) from our model fitting to better define relations within the first 1.8 km from open roads. Statistical inferences for all tests involving distance bands were based on transformed, weighted selection ratios; we considered probabilities ≤ 0.05 to be statistically significant.

Table 2. Characteristics of elk analysis units used in tests of elk distribution in relation to open road density, Starkey Experimental Forest and Range, Oregon, 1993–95.

Elk analysis unit	Area (ha)	Open road density (km/km^2)[a]	
		DEN1	DEN2
1	502	0.93	0.51
2	560	0.10	0.05
3	487	1.54	0.39
4	579	1.56	1.28
5	620	1.33	0.13
6	423	0.17	0.08
7	466	1.39	1.12
8	449	0.50	0.44
9	504	1.28	1.05
10	548	1.06	0.91
11	464	1.17	0.00
12	650	1.59	1.03
13	543	1.09	0.63
14	477	1.59	0.69
15	469	0.69	0.00

[a] Open road densities were calculated with 2 definitions of open roads: in DEN1, open roads included administrative roads and roads open to the public; in DEN2, open roads included only those roads open to the public.

Evaluating HE Model Predictions

To compare HE values predicted by the elk–road density model with observed values of HE from our study animals, we partitioned the study area into 15 elk analysis units that ranged in size from 423 to 650 ha. Units were placed within the 3 major subwatersheds in the study area (i.e., units did not cross subwatershed boundaries) and spanned a range of road densities (Table 2). Road densities were calculated using ARC/INFO software (Environmental Systems Research Institute 1990) by overlaying the roads vector layer with a polygon map layer of the elk analysis units. Open roads for our analysis were defined in 2 ways: (1) roads open to both public and occasional administrative use, where administrative use was limited to research activities and roads and facilities maintenance (DEN1); and (2) only those roads open to public use (DEN2).

To evaluate model predictions, we first calculated HE scores in each of our 15 units using 3 equations developed by Lyon (1983) as a "single nonlinear function." (The original equations reported in Hitchcock and Ager [1992:3] were in English units; here we present their metric equivalents.) The HE was determined as follows, where DEN = open road density in km/km^2: (1) if $\text{DEN} < 0.68$, $\text{HE} = 0.4 + (1 - 0.2688\ \text{DEN})^6 \times 0.6$; (2) if $0.68 \leq \text{DEN} < 1.24$, $\text{HE} = 0.486 + 0.1667(1.24 - \text{DEN})$; and (3) if

$1.24 \leq \text{DEN} \leq 3.72$, $\text{HE} = 0.104 + 0.154(3.72 - \text{DEN})$. We calculated 2 HE scores for each unit: the first (HE1) used the density of both administrative roads and those open to the public (DEN1), and the second (HE2) used the density of only those roads open to the public (DEN2). We included both administrative and open roads to more closely match the original definitions used when the elk–road models were developed; an open road was considered one accessible to motor vehicle traffic (Lyon 1979).

For regression analysis, we pooled elk locations (dependent variable) across animals within units (i.e., elk analysis units were sampling units; PROC REG, SAS Institute 1989). Spring and summer data were analyzed separately because prior investigation of elk in relation to open roads at Starkey revealed seasonal differences in distributions (M. M. Rowland, unpublished data). Numbers of elk locations were weighted first by unit area, because units were unequal in size (Table 2), and second by total number of elk locations per period, to account for varying numbers of elk locations among periods. We hypothesized that number of elk locations would be a linearly increasing function of HE, as predicted by the model.

Because locations were pooled across elk having an unequal number of locations, we explored the distribution of locations among grids. In no case did elk occur in a single unit in a period, nor did any individual elk dominate the analyses (e.g., by having as many as twice the mean number of locations for that sampling period). Mean number of units occupied by an elk in a sampling period ranged from 7.6 to 9.2 of the 15 units available. The median number of locations for elk either equaled (2 periods) or exceeded (4 periods) the mean (i.e., the distribution of number of locations was skewed more toward animals with fewer, rather than more, locations).

Measuring Effects of Other Environmental Variables

To address potentially confounding effects of other variables on our analysis of elk distribution in relation to roads, we calculated mean values (across all 30- × 30-m pixels) for 3 environmental variables in each distance band and elk analysis unit: tree canopy cover (%), defined as summed canopy closure for all trees with stem diameter >13 cm; slope (%); and elevation (m). We included these variables because these 3 were most likely to be correlated with locations of roads, and slope and canopy cover have previously been identified as significant variables in other analyses of elk habitat use (Edge et al. 1987, Unsworth et al. 1998). We computed Pearson correlation coefficients (PROC CORR; SAS Institute 1985) to test for associations between these 3 variables and variables used in our test of the elk–distance from roads hypothesis and in our evaluation of HE model predictions.

Simulating Effects of Road Density Patterns

Pattern and spatial distribution of roads may influence the relative area affected in relation to use by elk. We explored the relation between open road density, road pattern, and potential habitat loss by creating 9 hypothetical analysis units, each 10.4 km^2. We created a unique vector map for each unit by assigning 3 road densities (0.6, 1.9, and 3.1 km/km^2) across the units; each density was represented by 3 road patterns (even, random, and clumped). Roads were placed east–west and north–south, at right angles to one another (Fig. 2). For the even road pattern, roads were placed at regular intervals across the landscape; clumped roads were placed at 400-m intervals and were clustered in 1 corner of the units (Fig. 2). Starting points for randomly placed roads were drawn from a random numbers table. The vector maps were then rasterized and a 250-m horizontal buffer extended on both sides of all road segments to represent the zone of potential habitat loss to elk. This distance was selected based on work by Wisdom (1998) on the mean difference between all pixels at Starkey, in relation to distance to open roads, and pixels with elk locations. Finally, we calculated the proportion of area in the zone of potential habitat loss for each of the 9 units, as well as the size of the largest block of continuous habitat unaffected by roads.

RESULTS

Elk–distance from Roads Hypothesis

The ratio USEAVAIL differed among bands ($P < 0.001$) but not among animals ($P > 0.953$) in each sampling period under the ANOVA. For data pooled across years and seasons ($n = 4{,}660$ elk–band–sampling period combinations), the overall ANOVA accounted for >50% of the var-

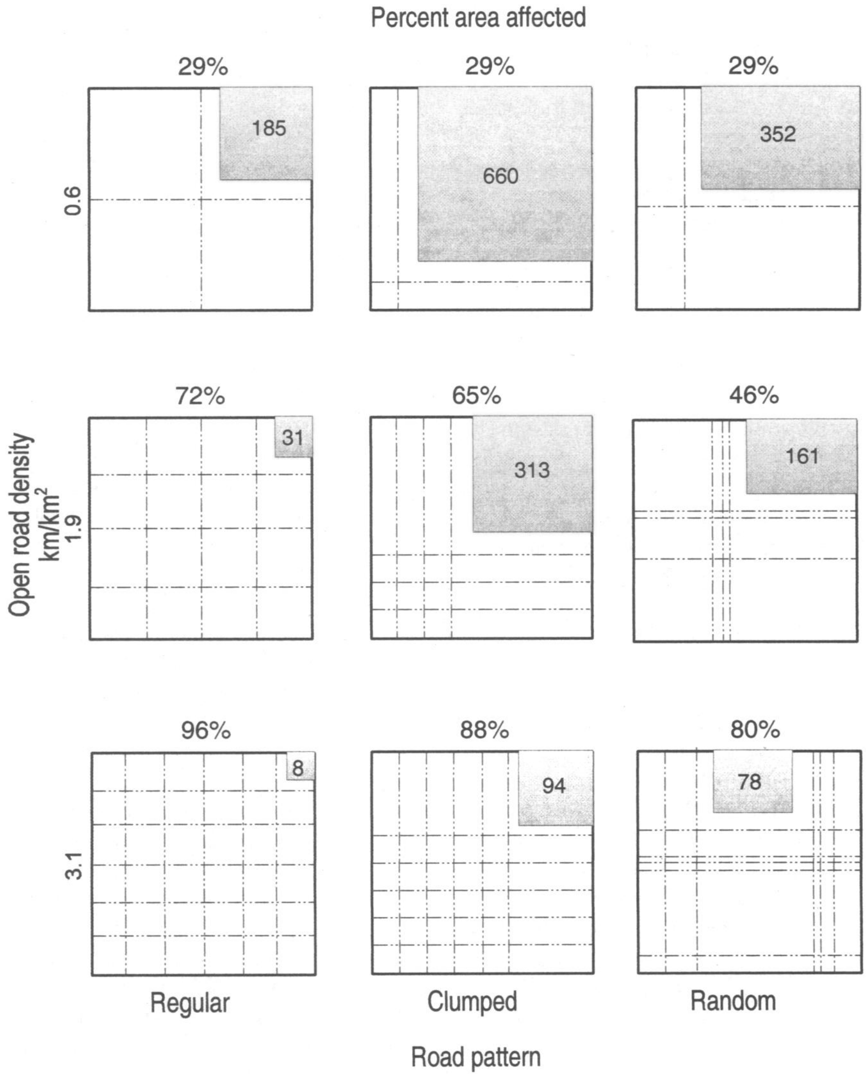

Fig. 2. Effect of road pattern and road density on area of potential habitat loss in 9 hypothetical elk analysis units. Buffer distance for road effect was 250 m on either side of roads (depicted by dashed lines). Shaded areas are largest continuous blocks of habitat unaffected by roads (ha). Total percentage of area affected by roads is reported above each unit.

iation in USEAVAIL ($F_{240,\ 4,419} = 22.99$, $r^2 = 0.56$, $P < 0.001$). The ratio USEAVAIL differed by distance band ($F_{19,\ 4,419} = 261.33$, $P < 0.001$), season ($F_{1,\ 4,419} = 76.06$, $P < 0.001$), season $\times$ distance band ($F_{19,\ 4,419} = 8.76$, $P < 0.001$), and year $\times$ distance band ($F_{38,\ 4,419} = 1.59$, $P = 0.012$), but not by year ($F_{2,\ 4,419} = 0.79$, $P = 0.455$) or animal ($F_{121,\ 4,419} = 0.64$, $P = 0.999$).

For ANOVAs run for each season separately, USEAVAIL differed in spring by distance band (linear term only; $F_{1,\ 2,071} = 1,819.09$, $P < 0.001$), but not by year ($F_{2,\ 2,071} = 0.70$, $P = 0.498$), animal ($F_{119,\ 2,071} = 0.41$, $P = 1.000$), or distance band $\times$ year ($F_{2,\ 2,071} = 1.10$, $P = 0.333$). In contrast to spring results, USEAVAIL differed among years in summer ($F_{2,\ 1,884} = 9.28$, $P < 0.001$; Fig. 3) and by distance band $\times$ year ($F_{2,\ 1,884} = 13.46$, $P < 0.001$). Similar to spring, selection ratios varied by distance band ($F_{1,\ 1,884} = 3,455.80$, $P < 0.001$), but not by animal ($F_{108,\ 1,884} = 0.25$, $P = 1.000$).

In the linear regression model developed for spring, selection ratios increased steadily as distance from road increased ($r^2 = 0.50$, $P < 0.001$; Fig. 3). For the 3 summer regression

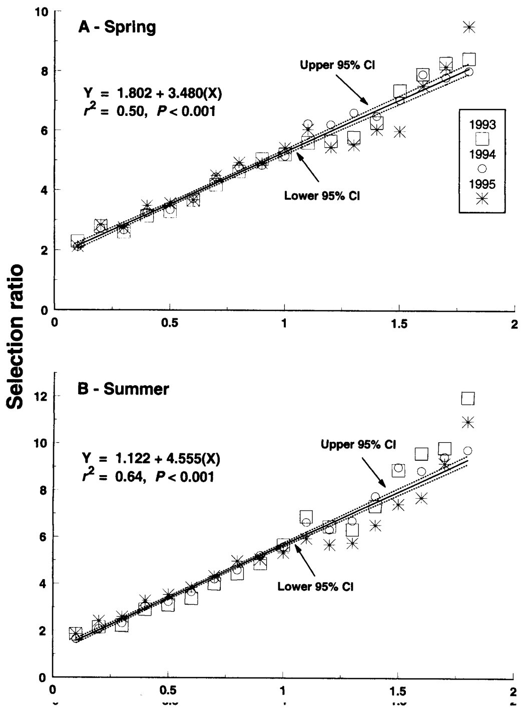

Fig. 3. Selection ratios (transformed and weighted USEAVAIL) of elk in relation to distance from open roads during spring (A) and summer (B), Starkey Experimental Forest and Range, Oregon, 1993–95 (see text for complete definition of USEAVAIL). Solid lines represent regression models for data pooled across years; dashed lines represent upper and lower bounds of the 95% confidence intervals for expected values (means) of USEAVAIL. Data points represent mean selection ratios observed for each year, by distance band. A USEAVAIL value of about 3 is equivalent to an untransformed selection ratio of 1 (i.e., no evidence of selection).

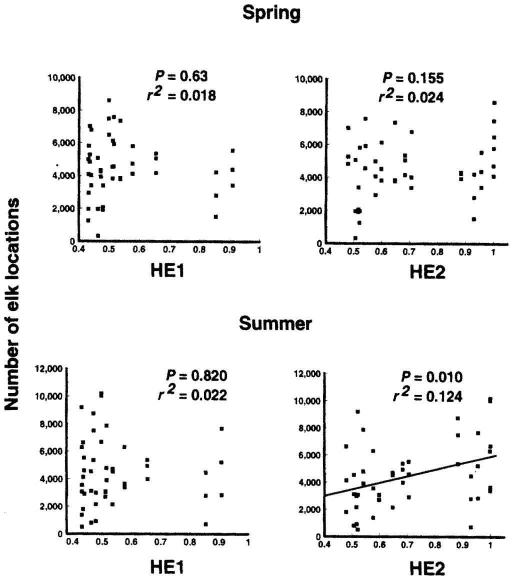

Fig. 4. Numbers of elk locations versus habitat effectiveness (HE) scores in 15 elk analysis units in the Starkey Experimental Forest and Range, Oregon, spring and summer 1993–95. The HE scores were calculated using 2 definitions of open roads: HE1 includes both administrative roads and roads open to the public; HE2 includes only roads open to the public (see text for equations for HE). Elk locations were weighted by size of units as well as number of locations per period, and pooled across animals. Regression equation for HE2 in summer: Y = 1,041 + 4,860X.

models, a positive, linear relation was found between USEAVAIL and distance band (r^2 = 0.64, $P < 0.001$; Fig. 3, combined model). Linear models for summer 1993 and 1994 were similar (P = 0.947), but 1995 differed from 1993 (P = 0.014) and from 1994 (P = 0.017). Slope of the 1995 model (3.97) was less than that of 1993 (4.88) or 1994 (4.76).

HE Model Predictions

Road densities among units ranged from 0.1–1.6 km/km^2 for DEN1, and 0 to 1.3 km/km^2 for DEN2 (Table 2). Corresponding HE1 scores ranged from 0.43 to 0.91 with both types of roads considered open, and from 0.48 to 1.00 for HE2 scores (Fig. 4). The maximum HE score (1.0) was associated with a wide range of elk numbers across the 6 sampling periods (6,497–10,190), as was the lowest score of 0.43 (507–9,202). We observed no linear relation ($P > 0.05$) between numbers of elk locations and HE, with the exception of HE2 in summer, when a weak correspondence was detected (r^2 = 0.124, P = 0.010, Y = 1,041 + 4,860X; Fig. 4).

Environmental Variables

Mean (±SE) slope was 21.5 ± 1.3% (n = 20, range = 13.2–31.8) across distance bands, and was positively correlated with distance to open roads (r = 0.994, $P < 0.001$). Slope averaged 18.1 ± 1.5% in the 15 elk analysis units (n = 15, range = 7.7–27.9); a weak, negative correlation was found between slope and open road density (r = −0.472, P = 0.076). Mean (±SE) elevation (1,355 ± 2.59 m; range = 1,328–1,374 m) decreased as distance to roads increased (r = −0.878, $P < 0.001$). Elevation in elk analysis units (1,358 ± 18.5 m; range = 1,210–1,458 m) was not correlated with open road density. Tree canopy cover was uniform ($P > 0.3$) across distance bands (28.0 ± 0.4%, range = 25.3–33.3%) and analysis units (27.6 ± 1.2%, range = 20.4–36.3%).

Simulating Road Density Patterns

Road pattern visibly affected potential habitat loss in our simulated elk habitats (Fig. 2). Regularly spaced roads had the greatest percentage of habitat influenced by roads, and randomly spaced roads the least. Moreover, clumped patterns produced comparatively larger continuous blocks of habitat unaffected by roads. For example, a clumped pattern of open roads at a density of 3.1 km/km^2 supported a block of unroaded habitat >3 times larger than that remaining in a unit with a regular pattern of roads and a density of only 1.9 km/km^2 (Fig. 2).

DISCUSSION

Elk–distance from Roads Hypothesis

Female elk within Starkey consistently selected areas away from open roads in both spring and summer, corroborating the empirical basis for the elk–roads model (Lyon 1983) and other studies (Hieb 1976, Perry and Overly 1977, Rost and Bailey 1979). Although we observed a strong linear increase in elk selection ratios throughout the range of distances used in regression analyses (0–1.8 km), variance of USEAVAIL increased as distance from roads increased. Presumably, as elk were further removed from road-related human activities, other factors (e.g., amount and quality of forage) more strongly influenced their distribution (Wisdom 1998, B. K. Johnson, unpublished data).

Precisely defining the distance at which road effects dissipated in our study area was infeasible due to the relative rarity of areas located far from roads (Table 1, Fig. 1B). The isolation of bands 1.9 and 2.0, which occurred in only 2 patches, may have rendered these areas largely unavailable to elk in our study. More than 40% of the occurrences of zero use in our data set were in the outer 2 bands, leading to depression of mean USEAVAIL values in these bands and less precise estimates of USEAVAIL as distance from roads increased.

We observed more pronounced selection away from roads in bands closest to roads during summer (as evidenced by lower values for USEAVAIL) and a steeper slope for the summer model compared to results for spring (Fig. 3). These seasonal differences could be explained by higher traffic rates during summer (M. J. Wisdom, unpublished data), when cattle are brought to Starkey and recreational use and research activities increase. These differences did not appear to be related to elk avoidance of cattle during summer, as cattle distributions within Starkey show no relation to distribution of open roads (B. K. Johnson, unpublished data). Also, stronger selection for areas away from roads in summer was not caused by roads being located disproportionately in more open habitat types (e.g., grasslands), where forage would be expected to cure earlier than in more shaded sites. Open roads at Starkey traverse a variety of habitat types; however, the relative proportions of vegetation types in which roads occur are identical to the relative proportions of these types within the study area as a whole (M. M. Rowland, unpublished data).

Differences among years in our linear models for summer were less easily explained. Selection ratios were similar among years until about 1.2 km, where models diverged for unknown reasons, resulting in a significant distance band × year interaction (Fig. 3). Although the summer 1995 model was statistically different from the 1993 and 1994 models, the pattern of increasing elk selection with increasing distance from open roads was qualitatively similar in all 3 years. Thus, annual differences in elk selections may have had little biological significance.

HE Model Predictions and Road Density

Despite the strong relation we detected between elk selection and distance from open roads, little or no significant relations appear to exist between number of elk locations and HE scores based on road densities. The 1 significant regression we obtained (summer-HE2) explained only 12% of the variation in elk numbers among analysis units. We believe this anomaly was largely due to differences in spatial scales associated with the 2 road metrics. That is, elk at Starkey appeared to demonstrate selection at the scale of our distance bands; however, selection away from roads was not detectable at the scale of our analysis units when HE values based on road density were used as a predictor. Apparently elk were able to select areas away from roads, yet still occur in large numbers in units with relatively high open road densities (e.g., 1.5 km/km^2). Similarly, Robel et al. (1993) found that inappropriate scale of model variables was likely to have caused the lack of correlation they observed between habitat suitability values for beaver (*Castor canadensis*) and densities of beaver colonies.

The conversion of data originally based on distance-to-roads to a larger scale based on open road densities may partially explain this contradiction. The original HE models for elk (Lyon 1979, 1983; Thomas et al. 1979) were developed using road densities, rather than distance-to-roads, because road density models could quantify habitat loss and account for the combined influence of multiple roads on elk (Lyon 1979). Furthermore, road densities were easily calculated for model input. Original linear models predicting HE from open road density assumed a cumulative effect of multiple roads on elk habitat, but such calculations may have overestimated losses in effective habitat, especially at higher road densities (Lyon 1979). Later models were less conservative and incorporated a "no overlap" rule, in which effects from one road were assumed to terminate at the midpoint between roads (Lyon 1983). Scaling up of the original distance-to-roads data in this manner, with its associated assumptions about elk behavior between roads and loss of habitat, may have obscured the true relation between elk distribution and roads. The use of distance bands may offer managers a more spatially appropriate scale for predicting road effects than do traditional road density models or analyses of habitats used versus those available (often described by sampling random points).

Our simulation of road pattern and its effect on potential habitat loss may offer further insight into lack of agreement between HE scores and elk numbers (Fig. 2). This exercise demonstrated that it is possible to have an area with relatively high road density, but habitat loss equivalent to an area with lower road density, depending on the spatial distribution of roads. We therefore recommend that spatial distribution of roads be considered when evaluating management units by HE scores, especially in areas with relatively few roads.

Size of our analysis units was a potential problem. Our units were small ($\bar{x}$ = 515 ha), whereas Lyon (1983) recommended analysis areas of 800–1,200 ha. We partitioned our study area to capture a range of road densities within Starkey, and in particular to obtain several units with densities <0.6 km/km^2, because HE declines rapidly in this portion of the model. However, we repeated our regression analysis with the study area subdivided into 7 larger analysis units ($\bar{x}$ = 1,100 ha), and obtained similar results (M. M. Rowland, unpublished data).

Population density may also affect elk response to roads at the scale of our HE model predictions; the relationships we detected are likely to change as animal density changes. Elk density in our study area was about 5.5/km^2. At lower densities, fewer elk may have remained in analysis units with high road densities, leading to improved performance of the model. However, the original elk–road density model implicitly assumed that predictions of HE were robust to variations in elk density.

Lastly, the lack of correlation between predicted and observed HE may be caused in part by the wide range of traffic rates associated with open roads at Starkey, and thus, differences in actual disturbance associated with roads in our 15 analysis units (Wisdom 1998). Some open road segments, such as those near the main entrance gate, receive far more traffic than segments in more remote portions of the study area, though all are open to the public.

Although models that predict changes in HE or selection ratios of elk in relation to roads are useful in analyzing effects of management prescriptions, a more fundamental question is how road-related disturbance influences elk fitness and survival, as well as plant community health. Vulnerability of elk to hunter harvest is closely associated with presence of roads (Christensen et al. 1991, Unsworth et al. 1993). In western Oregon, Cole et al. (1997) found that energetic costs of female Roosevelt elk (*C. e. roosevelti*) were reduced following road closures, and elk survival increased. Harassment of wildlife, such as that caused by traffic on roads, can lead to population reductions due to increased energetic costs and less access to favored resources (Geist 1978).

Furthermore, persistent road-mediated disturbance may lead to permanent shifts in habitat use by elk away from roads and thereby effect greater levels of herbivory in some sites. Large ungulates such as elk can have profound effects on ecosystem processes and components (Hobbs 1996, Augustine and McNaughton 1998). Given the widespread distribution of elk in the intermountain west, as well as the extensive road network on both public and private lands in this region, such effects could be substantial.

Environmental Variables

Correlation tests revealed that slope increased as distance to roads increased, and decreased with increasing open–road density. In addition, elevation was lower as distance to roads increased. These results reflect the location of most open roads in Starkey on gentle slopes and upper portions of drainages. Selection ratios for elk in the farthest bands may have been even higher had slopes not been steeper there, because elk often prefer gentler slopes (Hershey and Leege 1982, Irwin and Peek 1983, Edge et al. 1987). However, the range of differences in both slope and elevation in our study area were probably not ecologically significant for elk; mean elevation across our bands only varied from 1,328 to 1,374 m, and slope from 13 to 32%.

Tree canopy cover was consistent across Starkey and not correlated with distance to roads or open road density. Unsworth et al. (1998) found that elk in roaded areas tended to use habitats with greater canopy cover relative to unroaded areas. Some elk habitat models scale effects of roads on HE by security cover or tree canopy–cover classes (Lyon 1979, Roloff 1998). Such an adjustment was unnecessary, however, in our study area.

MANAGEMENT IMPLICATIONS

Our results support long-standing efforts by elk managers to mitigate negative effects of road-related human activities on elk distributions in forested ecosystems. We recommend retention of a road component in HE models for elk. However, our results suggest that a spatially explicit roads variable may be more appropriate, based on distance bands buffered from open roads, rather than road density alone. With the advent of GIS, assessment areas can easily be buffered into bands at prescribed distances from roads and assigned appropriate scores, as recommended in a draft habitat potential model for elk (Roloff 1998). Our study, combined with several previous studies, suggests that substantial shifts in elk distribution away from open roads are a widespread phenomenon. Because of the potential for effects of road densities at the landscape level on carrying capacity, managers and researchers would benefit from joint efforts to establish cause–effect relationships among elk distribution, open roads, and elk carrying capacity using large-scale management experiments replicated across a diversity of elk habitats in the western United States.

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